Parasitoid flies (Diptera, Tachinidae) in true crickets (Orthoptera, Grylloidea): New host records from Brazil, identification key to parasitoids, and revision of host-parasitoid interactions

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Academic editor: Ming Kai Tan | Received 6 July 2023 | Accepted 18 September 2023 | Published 22 January 2024

https://zoobank.org/0159CB15-EEC2-4533-8C2D-B461C409F33E

Citation: Gudin FM, Campos LD, Redü DR, de Mello FAG (2024) Parasitoid flies (Diptera, Tachinidae) in true crickets (Orthoptera, Grylloidea): New host records from Brazil, identification key to parasitoids, and revision of host-parasitoid interactions. Journal of Orthoptera Research 33(1): 41–58. https://doi.org/10.3897/jor.33.108456

Abstract

True crickets (Orthoptera, Grylloidea) are often parasitized by tachinid flies (Diptera, Tachinidae). However, the diversity of these parasitoids and their oviposition strategies remain unclear. Although some flies are specialized in locating crickets by their calling songs, such as the phonotactic fly Ormia ochracea (Bigot, 1889), a large portion of the tachinids that attack true crickets show different host search strategies and are adapted to parasitize other orthopteroid insects as well. However, these parasitoids have a complex and challenging taxonomy that precludes further improvement in the understanding of Tachinidae-Orthoptera interactions. Here, we described and illustrated seven new host records in Gryllidae and Phalangopsidae species from Brazil, including notes on the diagnostic characters of each parasitoid and host. An illustrated identification key to Tachinidae genera recorded in Grylloidea is also provided. Finally, all published records of Tachinidae parasitism in true crickets were revised and are presented in an annotated catalog in order to understand the host range and different oviposition strategies of each parasitoid lineage.

Keywords

chirping, endoparasitoids, Gryllidae, Neotropical Region, oviposition strategy, Phalangopsidae, phonotactics

Introduction

The cricket clade (Ensifera, Grylloidea) is one of the most diverse in Orthoptera, with more than 6,000 species distributed worldwide (Cigliano et al. 2023). These orthopterans are a subject of interest to the scientific community and have been commonly used as models in studies, including in those on biogeography (e.g., Vicente et al. 2017, Campos et al. 2021), bioacoustics (e.g., Huber et al. 1989, Hershberger 2021, Zefa et al. 2022), behavior (e.g., Ono et al. 2004, ter Hofstede et al. 2015, Lobregat et al.

2019), and speciation (e.g., Otte and Alexander 1983, Otte 1994, Shaw 1996, 2002, Ritchie and Garcia 2005). The most common parasitoids of true crickets are horsehair worms (Nematomorpha) (Hanelt et al. 2005), parasitic wasps (Hymenoptera, Chalcidoidea) (Noyes 2019), and tachinid flies (Diptera, Tachinidae) (Stireman et al. 2021).

The Tachinidae are well known as endoparasitoids of several groups of insects and other arthropods, showing a great variety of oviposition strategies (Stireman et al. 2021). Gravid females exhibit either direct oviposition, where they lay eggs on or within the host, or indirect oviposition, where they place eggs near the host (Nakamura et al. 2013). Direct oviposition consists of laying incubated or unincubated eggs on the host's cuticle or injecting them into the host itself. Indirect oviposition strategies include laying incubated micro-type eggs on the host's food, which are subsequently ingested by the host, as well as by depositing incubated membranous eggs with well-developed first-instar larvae that either wait or actively search for the host. Species of Coleoptera, Hemiptera, Hymenoptera, and Lepidoptera are frequently recorded as hosts of tachinids; however, some tachinid flies are specialized parasitoids of orthopteroid insects (Guimarães 1977, Arnaud 1978, Tschorsnig 2017).

In Orthoptera, the majority of tachinid parasitism records involve Acridoidea and Tettigonioidea (Crosskey 1973, 1976, 1984, Guimarães 1977, Arnaud 1978, Tschorsnig 2017), while such records are scarce in Grylloidea. Despite this, one of the most studied cases of parasitism in Tachinidae involves a specialized parasitoid of field crickets, the phonotactic fly *Ormia ochracea* (Bigot, 1889) (e.g., Gray et al. 2019). Ormiini flies are distributed worldwide and are parasitoids of Ensifera, locating their hosts by eavesdropping on the calling songs of males using well-developed tympanal organs in the prothorax (Lehmann 2003, Nihei 2015, Gudin and Nihei 2019). The prevalence and impact of *O. ochracea* parasitism

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have been reported as an important selective pressure in some populations of field crickets (Zuk et al. 2006), even shaping the density and distribution of different morphs in the population. However, only a few species of *Ormia* Robineau-Desvoidy, 1830, parasitize true crickets (Lehmann 2003).

Tachinidae species belonging to the New World genera *Anisia* Wulp, 1890, *Calodexia* Wulp, 1891, and *Exoristoides* Coquillett, 1897, are parasitoids of different orthopteroid insects, including a few records in true crickets (Rettenmeyer 1961b, O'Hara 2002, Weissman and Gray 2019). However, most of these species, especially in the Neotropical region, present a complex taxonomy, making it difficult to identify them accurately. This hinders the publication of host records and the expansion of our understanding regarding their host range.

Here, we present seven new host records for *Anisia*, *Calodexia*, and *Ormia* species reared from different species of Gryllidae and Phalangopsidae in Brazil. In addition, we provide an illustrated identification key to Tachinidae genera recorded in Grylloidea and a revision of grylloid hosts of Tachinidae in an annotated host catalog that includes an overview of the host use and oviposition strategies of their respective parasitoids.

Methods

The cricket specimens used in this study were originally collected from several localities in Brazil from 1989 to 1991 (except Anurogryllus (Urogryllus) toledopizai de Mello, 1988; see record and catalog below) and then kept in the laboratory to document further observations regarding their behavior. Meanwhile, tachinid flies emerged from them. Tachinidae and Grylloidea specimens were deposited in the collections of the Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, state of São Paulo, Brazil, and of the Laboratório de Insetos do Departamento de Biodiversidade e Bioestatística, Setor de Zoologia, Universidade Estadual Paulista "Júlio de Mesquita Filho" (BOTU), Botucatu, state of São Paulo, Brazil, respectively. When revising the host records, we found little information regarding the sex and number of parasitized crickets preserved in the BOTU collection (see records and catalog below). We identified the crickets using the taxonomic studies of de Mello (1992), Souza-Dias et al. (2015), Campos et al. (2017), and Redü and Zefa (2017). Photographs of crickets were taken using a Canon camera with a 100-mm macro lens. Serial photographs of different focuses were stacked using Helicon Focus v. 8.2.2. With the exception of Guabamima lordelloi de Mello, 1993, the photographed specimens are not those parasitized. When possible, we used images of specimens of the same species to illustrate the taxa, as the parasitized specimens were very damaged.

We identified the tachinids using keys to the New World genera of Blondeliini (Wood 1985) and the Central American genera of Tachinidae (Wood and Zumbado 2010). *Calodexia* species were identified using the keys proposed by Curran (1934a) and Rettenmeyer (1961b). The morphological terminology used in the descriptions of the specimens follows Cumming and Wood (2017). Photographs of emerged flies were taken with a Leica MC170 HD digital camera attached to a Leica MZ16 stereomicroscope using the software Leica Application Suite version 4.12.0, stacked with Helicon Focus, and edited in Gimp 2.10. James O'Hara kindly provided pictures of *Anisia gilvipes* (Coquillett, 1897) and *Exoristoides johnsoni* Coquillett, 1897, deposited in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC) to illustrate the identification key.

The host catalog follows an adapted format presented by Guimarães (1977) and Arnaud (1978). Species are listed alphabetically according to their respective biogeographical regions with valid names accompanied by authorship. Species names of grylloid hosts are followed by author, year of publication, page number, locality, respective tachinid parasitoid, and notes on the record. When necessary, we included comments and emendations regarding taxonomic nomenclature and reliability of the record in square brackets. To update the catalog of grylloid hosts, only published articles were considered, not including dissertations and theses. We also did not consider the use of sound traps broadcasting cricket calling songs to attract phonotactic orienting parasitoids as a host record. Moreover, as there are many studies on the host-parasitoid interactions of O. ochracea and to not unnecessarily inflate the catalog, we included only the first records in different localities to cover the distribution of host records. The original literature was checked to ensure the accuracy of the dates, titles, pagination, names, and localities. The classification of Tachinidae follows O'Hara et al. (2020), and the classification of Grylloidea follows the Orthoptera Species File (Cigliano et al. 2023).

Results

New host records

Record of Anisia Wulp, 1890, in Aracamby de Mello, 1992

In July 1990, one female of *Anisia* (Fig. 1A–C) was reared from an adult of *Aracamby* (Fig. 1D–G) collected from Caraguatatuba, São Paulo, Brazil. Only one *Anisia* species has been recorded in Brazil: *A. facialis* (Townsend, 1927), described from Itaquaquecetuba, São Paulo (Townsend 1927), and reared from Forficulidae (Dermaptera) (Parker 1953). Our specimen, however, differs from it by having the upper half of the fronto-orbital plate, scutum, and scutellum covered with slight golden pruinosity and wings hyaline.

The cricket specimen belongs to an undescribed species of *Aracamby* geographically close to *A. picinguabensis* de Mello, 1992; however, the tympana are absent on the foretibia, and the genital structures are somewhat different, mainly in the pseudepiphallic sclerite.

Record of Calodexia Wulp, 1891, and Ormia ochracea (Bigot, 1889) in Anurogryllus (Urogryllus) toledopizai (de Mello, 1988)

On November 21, 2012, one male of Calodexia (Fig. 2A–C) was reared from a male of A. (U.) toledopizai (Fig. 2J–M) collected from Canguçu, Rio Grande do Sul, Brazil. On December 30, 2013, a male and a female of O. ochracea (Fig. 2D-I) were reared from two males of A. (U.) toledopizai collected in São Lourenço do Sul, Rio Grande do Sul, Brazil. The male of Calodexia does not run to any species included in the identification keys of Curran (1934a) and Rettenmeyer (1961b). The head and thorax are covered with silver pruinosity; scutum with well-defined and separated vitta, legs yellow, and abdomen yellow on sides with a large brown vitta widening toward the tip and covering almost the entire dorsal surface of tergite 4. Ormia ochracea can be identified by having ocelli absent, parafacial bare, and tegula black; females with fronto-orbital plate swollen and frontal profile strongly arcuate; males with only one callosity on costal vein between veins R_1 and R_{2+3} ; and male syncercus with apex straight in lateral view (Sabrosky 1953, Tavares 1965).

Details regarding the taxonomy and distribution of A. (U.) toledopizai can be found in Redü and Zefa (2017).

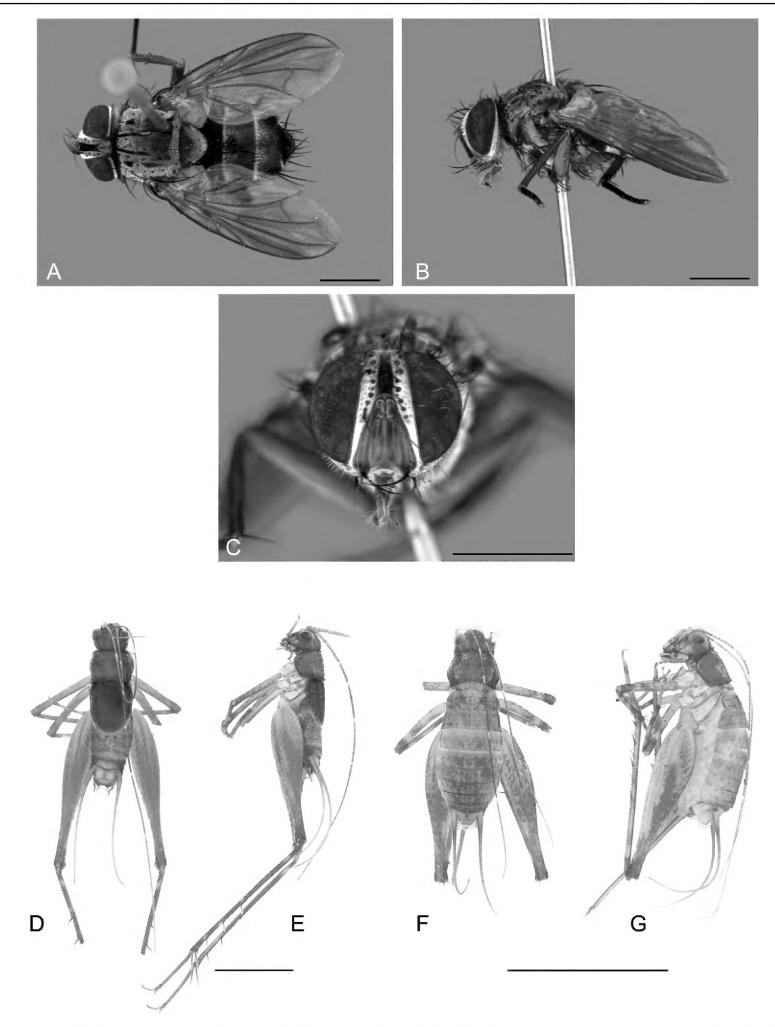


Fig. 1. Anisia Wulp, 1890, reared from Aracamby de Mello, 1992 (Phalangopsidae). A–C. Anisia female, dorsal habitus, lateral habitus, and head in frontal view, respectively; D, E. Aracamby male, dorsal and lateral habitus, respectively; F, G. Aracamby female, dorsal and lateral habitus, respectively. Scale bars: 2 mm (A–C); 5 mm (D–G).

Record of Calodexia cf. fasciata Curran, 1934a, in Eidmanacris Chopard, 1956

In August 1991, one female of *C.* cf. *fasciata* (Fig. 3A–C) was reared from an adult of *Eidmanacris* (Fig. 3D–G) collected from Apiaí, São Paulo, Brazil. *Calodexia fasciata* was described from Barro Colorado Island, Panama, based on a series of females (Curran 1934a). Our specimen runs to *C. fasciata* in the identification keys of Curran (1934a) and Rettenmeyer (1961b) and fits the characters of the type series, such as the head, thorax, and abdomen covered with silver pruinosity but with an ochraceous tinge on fronto-orbital plate, scutum, and dorsal surface of abdomen; scutum with inner

postsutural vittae fused; acrostichal setae 1:1; lateral surface of thorax with sparse black setulae and legs black. This species also does not have setae on the ventral surface of the mid tibia, which was not possible to verify in our specimen as almost all the legs were lost.

The specimen of *Eidmanacris* from Apiaí belongs to an undescribed species. Its morphological traits, such as the large dorsal band of the abdomen, supra anal plate latero-posterior projections, forewings with apex rounded, and metanotum covered by bristles, allow us to place this species within *Eidmanacris* Clade A (Campos et al. 2021). In contrast to other *Eidmanacris* species found inside holes and caves, the species from Clade A are found in litter and are present only in the Atlantic Forest.

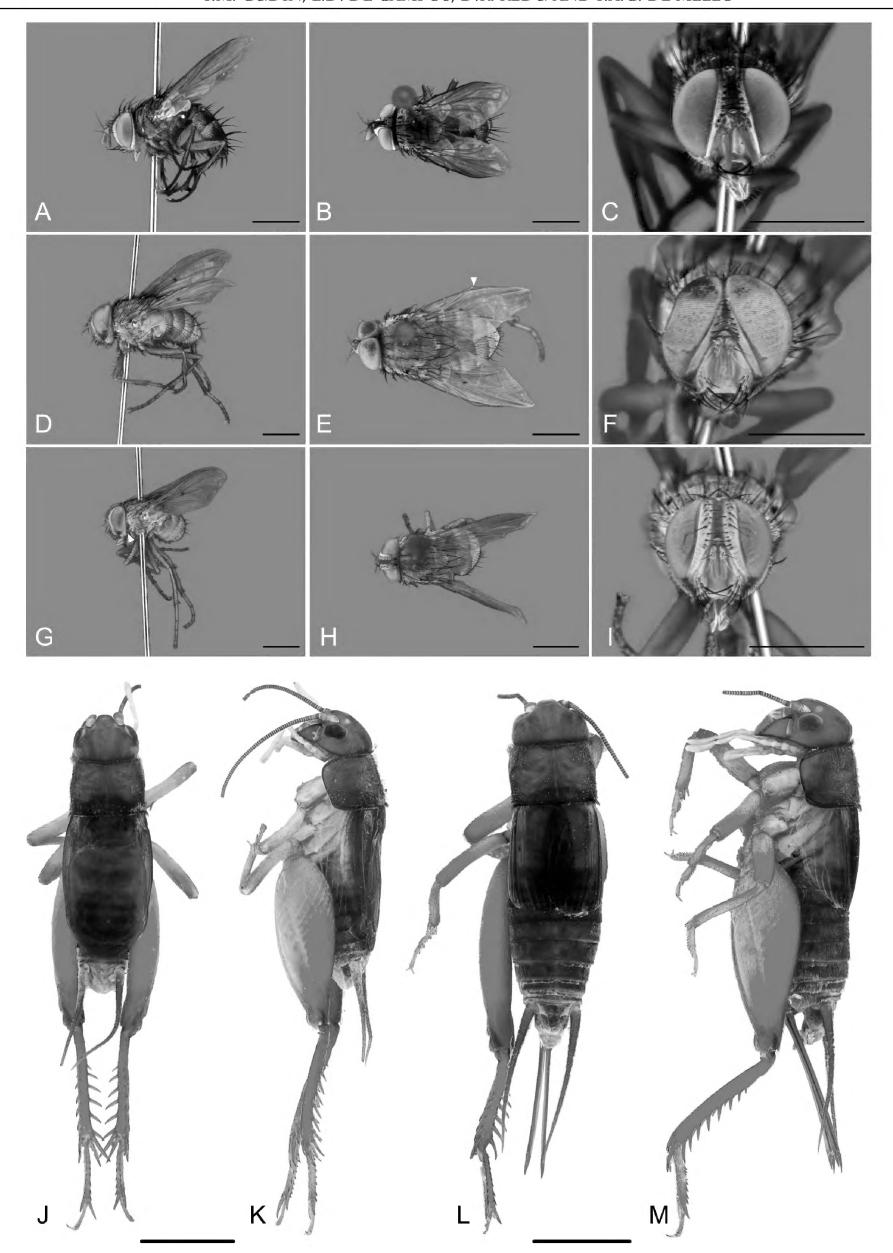


Fig. 2. Calodexia Wulp, 1891, and Ormia ochracea (Bigot, 1889), reared from Anurogryllus (Urogryllus) toledopizai (de Mello, 1988) (Gryllidae). A–C. Calodexia male, lateral habitus, dorsal habitus, and head in frontal view, respectively; D–F. Ormia ochracea male, lateral habitus, dorsal habitus, and head in frontal view, respectively, with white arrow showing callosity on costal vein; G–I. Ormia ochracea female, lateral habitus, dorsal habitus, and head in frontal view, respectively, with white arrow showing the position of the inflated basisternum and tympanal membrane; J, K. Anurogryllus (U.) toledopizai male, dorsal and lateral habitus, respectively; L, M. Anurogryllus (U.) toledopizai female, dorsal and lateral habitus, respectively. Scale bars: 2 mm (A–I); 5 mm (J–M).

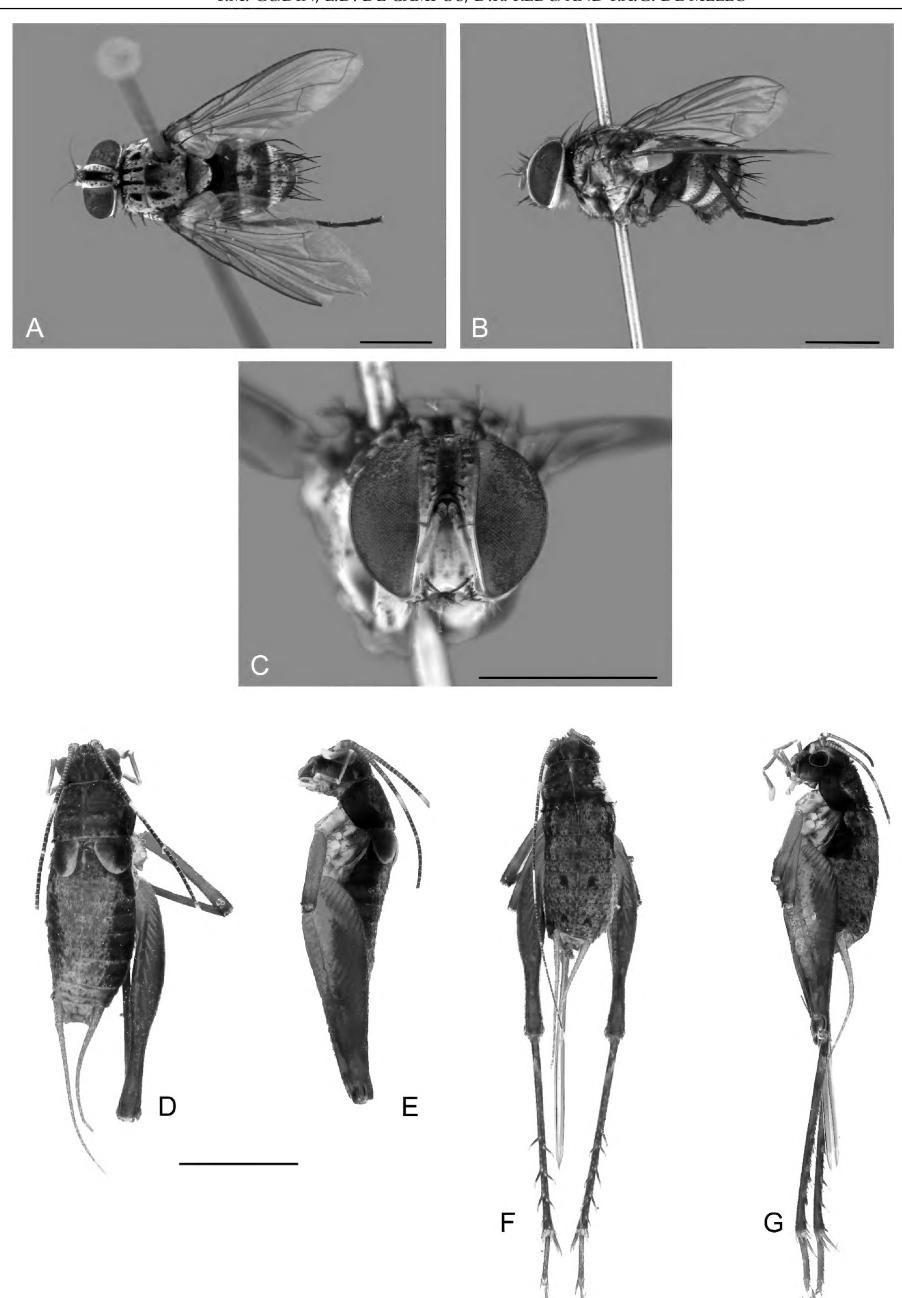


Fig. 3. Calodexia cf. fasciata Curran, 1934a, reared from Eidmanacris Chopard, 1956 (Phalangopsidae). A–C. Calodexia cf. fasciata female, dorsal habitus, lateral habitus, and head in frontal view, respectively; D, E. Eidmanacris male, dorsal and lateral habitus, respectively; F, G. Eidmanacris female, dorsal and lateral habitus, respectively. Scale bars: 2 mm (A–C); 5 mm (D–G).

Record of *Calodexia* cf. *flavipes* (Schiner, 1868) in *Aracamby* de (1961b), such as the head, scutum, and abdomen covered with golden pruinosity; ocellar setae weak; scutum with inner postsu-

In December 1990, two males of *Calodexia* cf. *flavipes* (Fig. 4A–C) were reared from adults of *Aracamby* (Fig. 4D–G) collected from Matinhos, Paraná, Brazil. *Calodexia flavipes* was described from Brazil based on a single male (Schiner 1868). Our specimens run to *C. flavipes* in the identification keys of Curran (1934a) and Rettenmeyer (1961b) and fit the characters of the holotype of *C. flavipes* as described by Aldrich (1929), such as the head, scutum, and abdomen covered with golden pruinosity; scutum with inner postsutural vittae fused; legs black with femora yellow at basal half; and abdomen slender and yellow with dark brown vitta. However, our specimens do not have yellow setulae on the ventral surface of the mid- and hind femora.

Similar to the previous record, these crickets belong to an undescribed *Aracamby* species. The main characters that set them apart from the species already described are mainly in the male genitalia and female copulatory papilla.

Record of Calodexia cf. flavipes (Schiner, 1868) in Phalangopsidae

On June 29, 1989, three males of *C*. cf. *flavipes* (Fig. 5A–C) were reared from adults of unidentified Phalangopsidae collected from Boracéia Biological Station, Salesópolis, São Paulo, Brazil. Our specimens fit the same characters as those presented in the record described above.

It was possible to identify the crickets only at the family level because of their poor condition.

Record of *Calodexia* cf. *insolita* Curran, 1934b, in *Pizacris* Souza-Dias & Desutter-Grandcolas, 2015

In July 1989, two females of *C.* cf. *insolita* (Fig. 6A–C) were reared from adults of *Pizacris* (Fig. 6E–G) collected from São Fidélis, Rio de Janeiro, Brazil. *Calodexia insolita* was described from Kartabo, Guyana, based on a single female (Curran 1934b). Our specimens run to *C. insolita* in the identification keys of Curran (1934b) and Rettenmeyer (1961b) and fit the characters of the holotype female, such as the head, thorax, and abdomen covered with silver pruinosity, but with an ochraceous tinge on frontoorbital plate and scutum; ocellar setae absent; scutum with inner postsutural vittae fused and with postsutural pruinose vitta narrow; and legs black with femora yellow at basal half. We also found three females of *Stylogaster* Macquart, 1835 (Diptera: Conopidae), reared from *Pizacris* in the same locality (Fig. 6D).

The locality of the parasitized cricket is close to the type locality of *Pizacris carioca* Souza-Dias & Desutter-Grandcolas, 2015, in Rio de Janeiro. However, because of its poor condition, it was not possible to determine whether it is the same or an undescribed species.

Record of Calodexia cf. venteris Curran, 1934a, in Guabamima lordelloi, de Mello, 1993

In July 1989, one male of *C.* cf. *venteris* (Fig. 7A–C) was reared from a male of *G. lordelloi* (Fig. 7D–G) collected from Fazenda Farol, Mucuri, Bahia, Brazil. *Calodexia venteris* was described from Barro Colorado, Panama, based on a series of females (Curran 1934a). Our specimen runs to *C. venteris* in the identification keys of Curran (1934a) and Rettenmeyer (1961b) and fits the characters of the type series and the males described by Rettenmeyer

(1961b), such as the head, scutum, and abdomen covered with golden pruinosity; ocellar setae weak; scutum with inner postsutural vittae fused; lateral surface of thorax with sparse white setulae; and abdomen slender and yellow with pruinose bands on basal half of tergites, without dark brown vitta. This species also has important characters in the legs, but it was not possible to verify this in our specimen as all legs were lost.

Of the parasitized crickets recorded in this study, the specimen of *G. lordelloi* was the only one in good enough condition to be photographed. Moreover, it is the holotype of this species (de Mello 1993) (Fig. 7D, E), which is deposited in the MZSP.

Identification key to Tachinidae genera recorded in Grylloidea

To date, species from four Tachinidae genera have been recorded with certainty as parasitoids of true crickets (see catalog below): Anisia and Calodexia (Exoristinae: Blondeliini), Exoristoides (Tachininae: Polideini), and Ormia (Tachininae: Ormiini). Anisia and Ormia include 21 and 27 valid species, respectively, distributed throughout the Nearctic and Neotropical regions; Calodexia includes 40 valid species and is endemic to the Neotropical region; and Exoristoides includes five valid species that occur in the Nearctic region and Central America (Wood and Zumbado 2010, O'Hara et al. 2020). These genera can be identified by the following character sets, adapted from the identification key of Wood and Zumbado (2010):

Annotated catalog of grylloid hosts of Tachinidae

At least ten species of Tachinidae in four genera of the New World are currently recorded as parasitoids of at least 31 species of the families Gryllidae, Oecanthidae, and Phalangopsidae

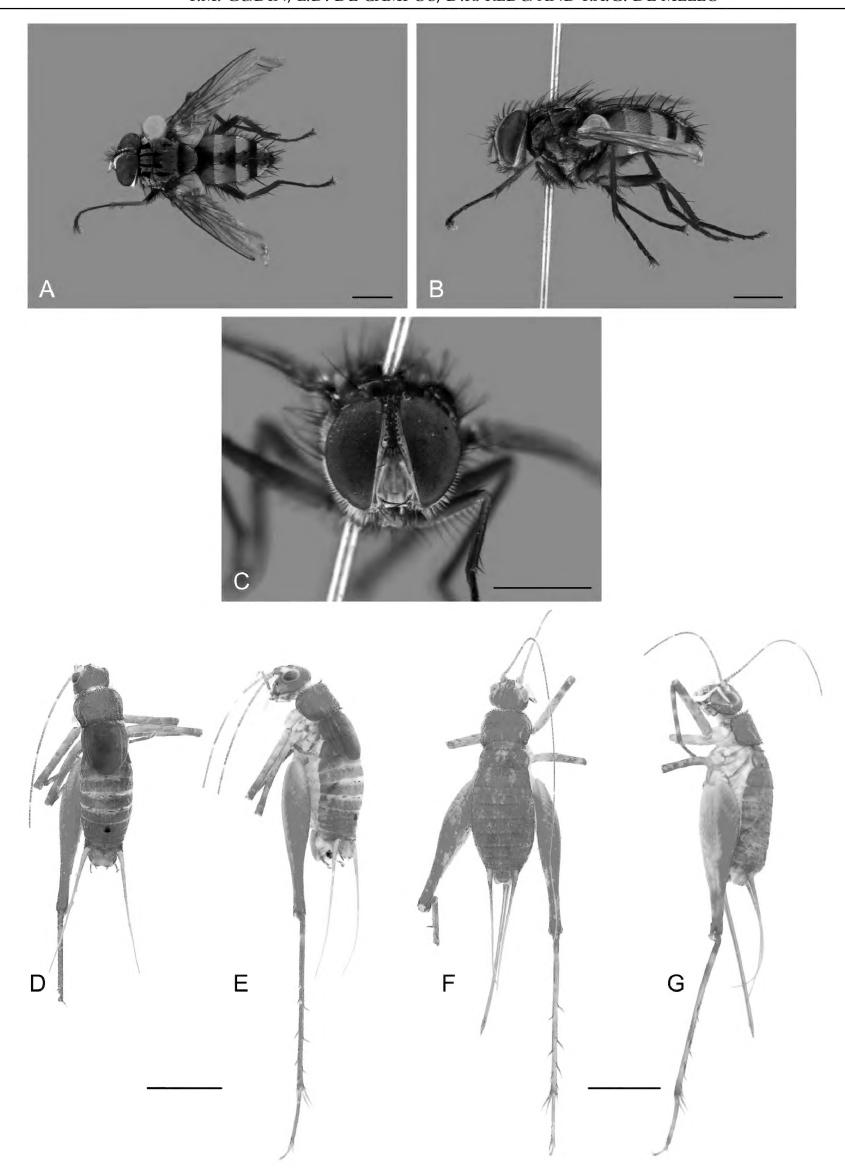


Fig. 4. Calodexia cf. flavipes (Schiner, 1868) reared from Aracamby de Mello, 1992 (Phalangopsidae). A-C. Calodexia cf. flavipes male, dorsal habitus, lateral habitus, and head in frontal view, respectively; D, E. Aracamby male, dorsal and lateral habitus, respectively; F, G. Aracamby female, dorsal and lateral habitus, respectively. Scale bars: 2 mm (A–C); 5 mm (D–G).

(Table 1). To the best of our knowledge, there are currently no published records of tachinid parasitism in true crickets in biogeographical regions other than the Nearctic and Neotropical regions. The parasitism records of O. ochracea in Teleogryllus (Teleogryllus) oceanicus (Le Guillou, 1841) in Hawaii actually involve two exotic the laboratory are indicated in the catalog.

species: O. ochracea was introduced in Hawaii probably from western North American populations of the United States of America, and T. (T) oceanicus was introduced from Australia (Gray et al. 2019). Parasitism records obtained through artificial infestation in

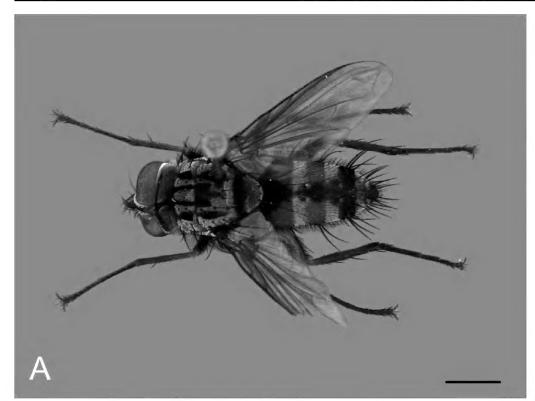






Fig. 5. Calodexia cf. flavipes (Schiner, 1868) reared from an unidentified Phalangopsidae. A–C. Calodexia cf. flavipes male, dorsal habitus, lateral habitus, and head in frontal view, respectively. Scale bars: 2 mm (A–C); 5 mm (D–G).

Australasian Region

Teleogryllus (Teleogryllus) oceanicus (Le Guillou, 1841) (Gryllidae, Gryllinae, Gryllini) [introduced species]

Zuk et al. (1993: 340, record from Hilo, Hawaii County, Hawaii, United States of America, parasitoid as *Ormia ochracea* (Bigot) [introduced species]); Zuk et al. (1998: 167, records from Hilo (Hawaii County), Manoa (Honolulu County) and Research Station (Kauai County), Hawaii, United States of America, parasitoid as *O. ochracea* [introduced species]).

Nearctic Region

Acheta domesticus (Linnaeus, 1758) (Gryllidae, Gryllinae, Gryllini)

Wineriter and Walker (1990: 625, record [artificial infestation] from Gainesville, Alachua County, Florida, United States of America, parasitoid as *Ormia ochracea* (Bigot)); Adamo (1998: 530, record [artificial infestation] from Halifax, Nova Scotia, Canada, parasitoid as *O. ochracea*); Paur and Gray (2011: 148, record [artifi-

cial infestation] from Northridge, Los Angeles, Los Angeles County, California, United States of America, parasitoid as *O. ochracea*).

Anurogryllus (Anurogryllus) arboreus Walker, 1973 (Gryllidae, Gryllinae, Gryllini)

O'Hara (2002: 159, record from Gainesville, Alachua County, Florida, United States of America, parasitoid as *Exoristoides johnsoni* Coquillett).

Anurogryllus (Anurogryllus) muticus (de Geer, 1773) (Gryllidae, Gryllinae, Gryllini)

Weaver and Sommers (1969: 342, record from Louisiana, United States of America, parasitoids as unidentified *Exoristoides* Coquillett and Theresiini [=Dexiini. Species of Dexiini are generally parasitoids of coleopteran and lepidopteran larvae (Guimarães 1977, Arnaud 1978). Dexiini females are ovoviviparous, laying incubated membranous eggs with well-developed first instar larvae that actively search for the host. Although this record may be reliable, the parasitism of a Dexiini specimen on a grylloid host is probably accidental, as Dexiini larvae are commonly deposited in litter]).

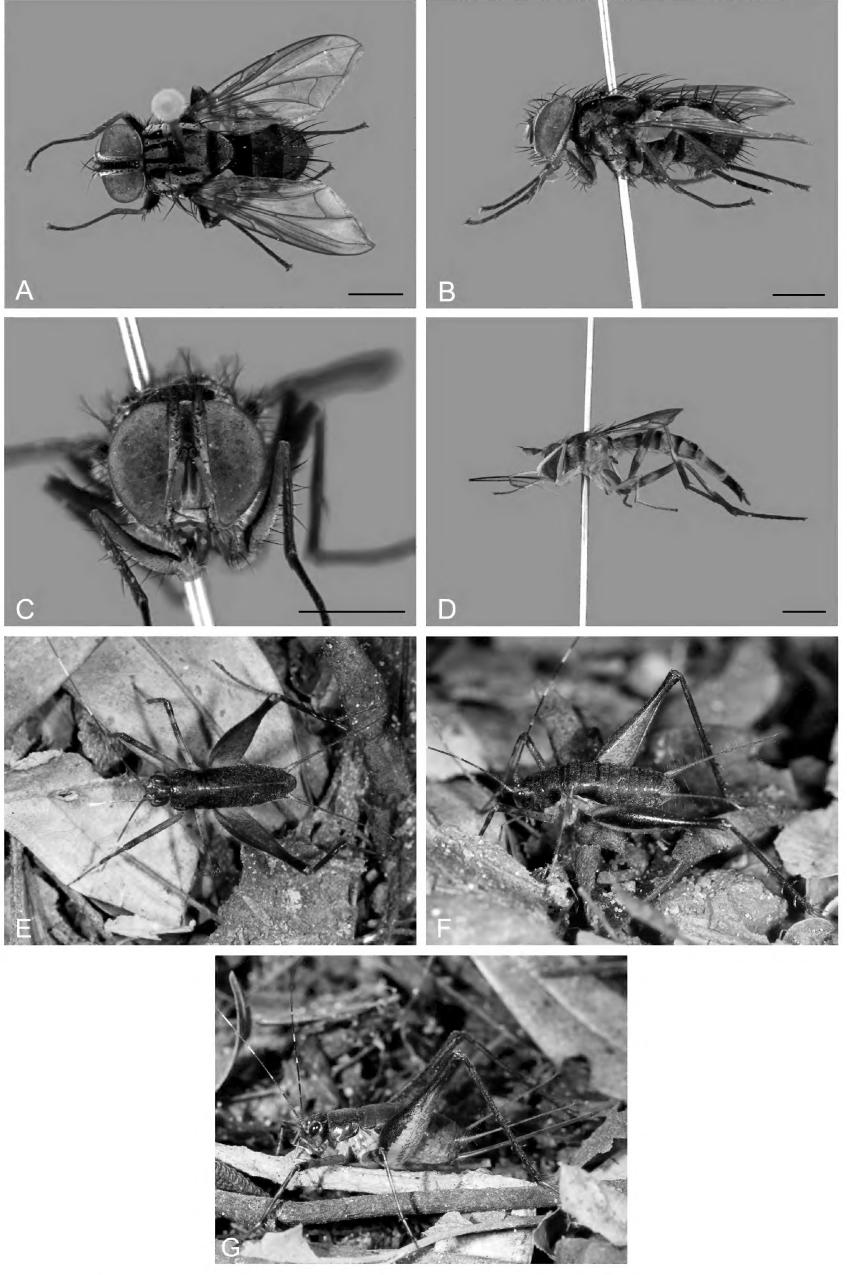


Fig. 6. Calodexia cf. insolita Curran, 1934b (Tachinidae), and Stylogaster Macquart, 1835 (Conopidae), reared from Pizacris Souza-Dias and Desutter-Grandcolas, 2015 (Phalangopsidae). A–C. Calodexia cf. insolita female, dorsal habitus, lateral habitus, and head in frontal view, respectively; **D.** Stylogaster female, lateral habitus; **E, F.** Pizacris male, dorsal and lateral habitus, respectively; **G.** Pizacris female, lateral habitus. Scale bars: 2 mm (A–D); 5 mm (E–G).

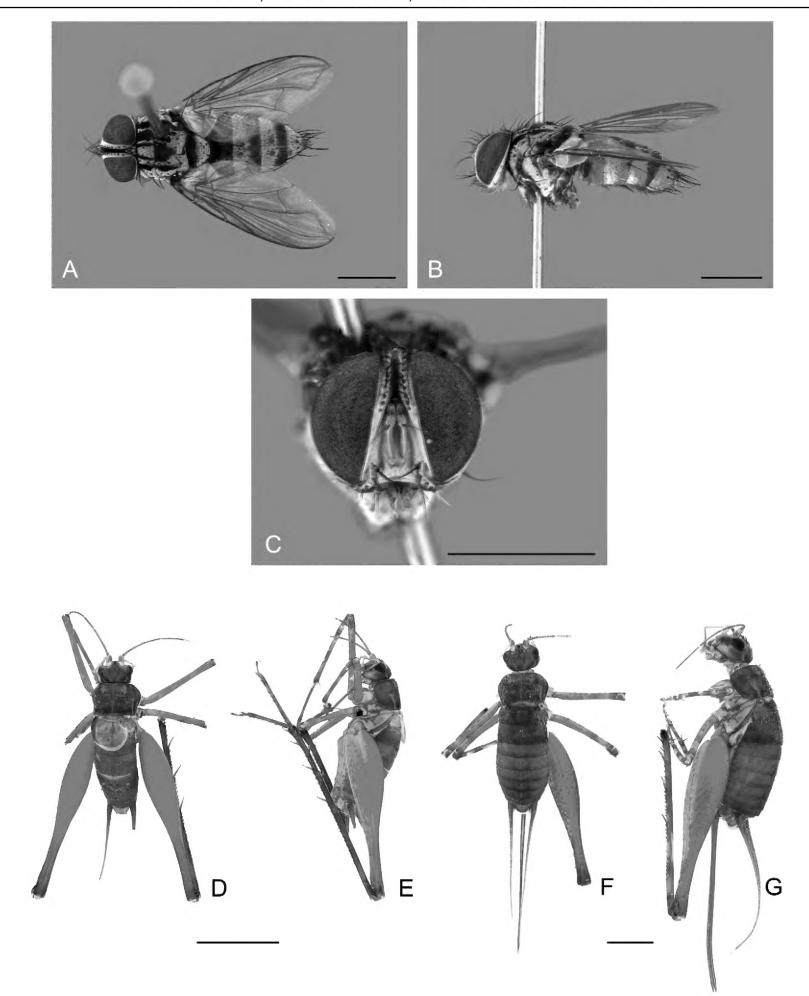


Fig. 7. Calodexia cf. venteris Curran, 1934a, reared from *Guabamima lordelloi* de Mello, 1993 (Phalangopsidae). A–C. Calodexia cf. venteris male, dorsal habitus, lateral habitus, and head in frontal view, respectively; **D**, **E**. *Guabamima lordelloi* holotype male, dorsal and lateral habitus, respectively; **F**, **G**. *Guabamima lordelloi* female, dorsal and lateral habitus, respectively. Scale bars: 2 mm (A–C); 5 mm (D–G).

Gryllus (Gryllus) armatus Scudder, 1902 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 119, records from Havasu Lake (San Bernardino County, California), and Wenden (La Paz County, Arizona), United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) assimilis (Fabricius, 1775) (Gryllidae, Gryllinae, Gryllini)

Reinhard (1922: 72, record from College Texas, Brazos County, United States of America, parasitoid as *Ormia ochracea* (Bigot)); Severin (1926: 224, record from South Dakota, United States of

America, parasitoid as *Exoristoides johnsoni* Coquillett); Aldrich (1932: 24, records from Sacramento (Sacramento County), and Winters (Yolo County), California, United States of America, parasitoid as *E. johnsoni*); Thomson et al. (2012: 44, record [artificial infestation] from Bastrop County, Texas, United States of America, parasitoid as *O. ochracea*).

Gryllus (Gryllus) bimaculatus de Geer, 1773 (Gryllidae, Gryllinae, Gryllini)

Adamo et al. (1995: 270, record [artificial infestation] from Ithaca, Tompkins County, New York, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

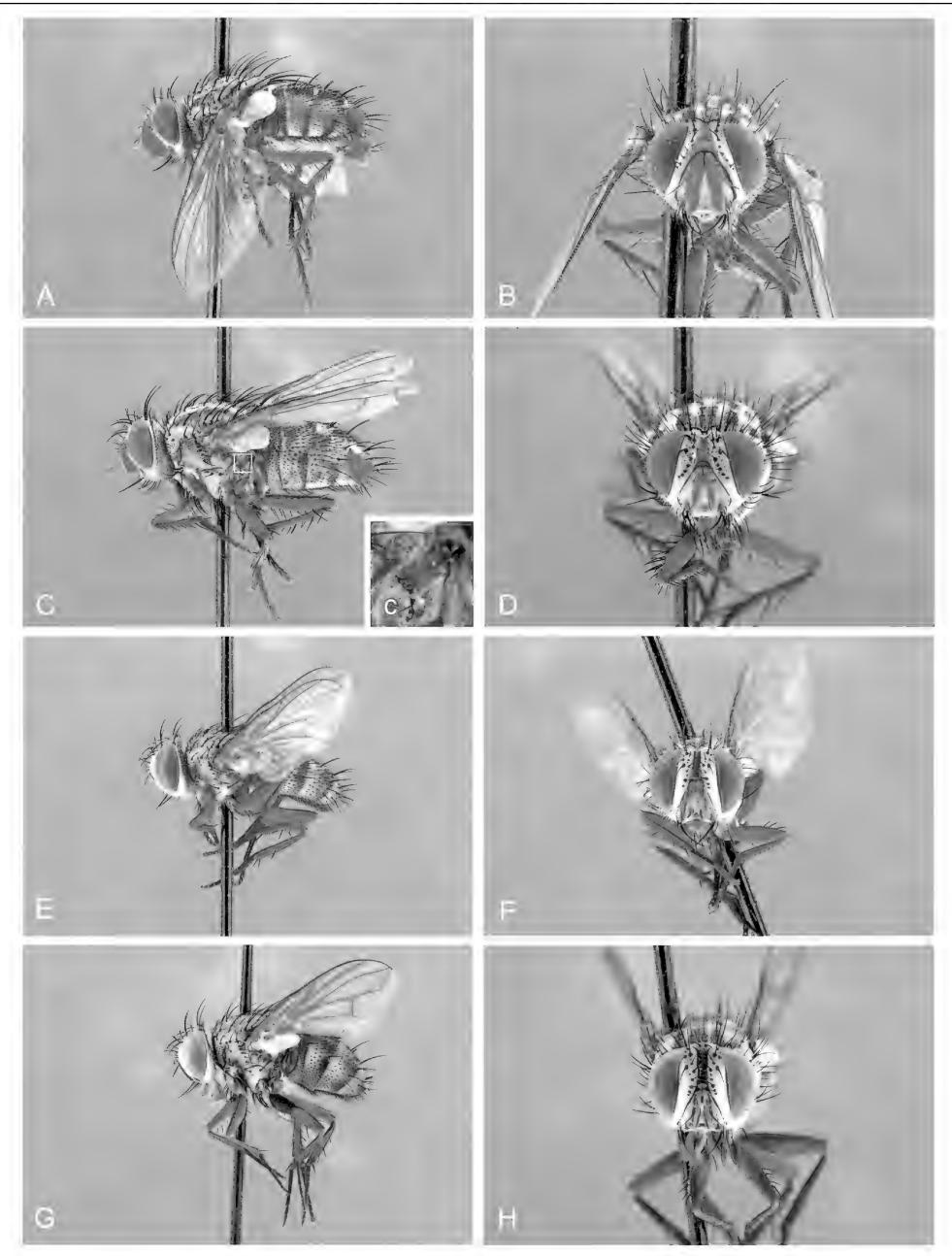


Fig. 8. Exoristoides johnsoni Coquillett, 1897 (Polideini), and Anisia gilvipes (Coquillett, 1897) (Blondeliini), deposited in CNC. A, B. Exoristoides johnsoni male, lateral and dorsal habitus, respectively; C, D. Exoristoides johnsoni female, lateral and dorsal habitus, respectively, with detail (c) of metathoracic spiracle; E, F. Anisia gilvipes male, lateral and dorsal habitus, respectively. Images originally lacking scales.

Table 1. List of tachinids that are parasitoids of Grylloidea and their respective hosts according to biogeographical regions. Details about the records, localities, and respective references can be found in the host catalog in the main text. New hosts recorded in this study are marked with an asterisk.

Tachinidae species	Grylloidea hosts
Australasian Region	T-111 (T-111)
Ormia ochracea	Teleogryllus (Teleogryllus) oceanicus
Nearctic Region Anisia gilvipes	Unidentified Grylloidea
Anisia sp.	Gryllus sp.
Exoristoides johnsoni	Anurogryllus (Anurogryllus) arboreus
Exoristolues Johnsoni	Anurogryllus (Anurogryllus) muticus
	Gryllus (Gryllus) assimilis
	Gryllus (Gryllus) integer
	Gryllus (Gryllus) montis
	Gryllus (Gryllus) pennsylvanicus
	Gryllus (Gryllus) saxatilis
	Gryllus (Gryllus) veletis
	Gryllus (Gryllus) vocalis
Ormia dominicana	Hapithus (Orocharis) luteolira
Ormia ochracea	Acheta domesticus
	Gryllus (Gryllus) armatus
	Gryllus (Gryllus) assimilis
	Gryllus (Gryllus) bimaculatus
	Gryllus (Gryllus) cohni
	Gryllus (Gryllus) firmus
	Gryllus (Gryllus) integer
	Gryllus (Gryllus) lightfooti
	Gryllus (Gryllus) lineaticeps
	Gryllus (Gryllus) longicercus
	Gryllus (Gryllus) montis
	Gryllus (Gryllus) multipulsator
	Gryllus (Gryllus) ovisopis
	Gryllus (Gryllus) rubens
	Gryllus (Gryllus) saxatilis
	Gryllus (Gryllus) staccato
	Gryllus (Gryllus) texensis
	Gryllus (Gryllus) vocalis
Unidentified Dexiini	Anurogryllus (Anurogryllus) muticus
Unidentified Tachinidae	Gryllus (Gryllus) brevicaudus
Neotropical Region	Giffine (Giffine) evereuman
Anisia sp.	Aracamby sp.*
Calodexia cf. flavipes	Aracamby sp.*
	Unidentified Phalangopsidae*
Calodexia cf. fasciata	Eidmanacris sp. *
Calodexia cf. insolita	Pizacris sp.*
Calodexia interrupta	Ponca venosa
Calodexia cf. venteris	Guabamima lordelloi*
Calodexia sp.	Anurogryllus (Urogryllus) toledopizai
	Eneoptera sp.
	Unidentified Grylloidea
	Unidentified Phalangopsidae
Ormia depleta	Anurogryllus sp.
Ormia ochracea	Anurogryllus (Urogryllus) toledopizai
	Gryllus (Gryllus) assimilis
	Gryllus (Gryllus) cohni
	Gryllus (Gryllus) multipulsator
	Gryllus (Gryllus) staccato
	Gryllus sp.

Gryllus (Gryllus) brevicaudus Weissman, Rentz & Alexander, 1980 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 40, record from Stanford University's Jasper Ridge Biological Preserve, San Mateo County, California, United States of America, parasitoid as unidentified Tachinidae).

Gryllus (Gryllus) cohni Weissman, Rentz & Alexander, 1980 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 168, record from Agua Fria, Yavapai County, Arizona, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (*Gryllus*) *firmus* Scudder, 1902 (Gryllidae, Gryllinae, Gryllini)

Wineriter and Walker (1990: 625, record [artificial infestation] from Gainesville, Alachua County, Florida, United States of America, parasitoid as *Ormia ochracea* (Bigot)); Thomson et al. (2012: 44, record [artificial infestation] from Bastrop County, Texas, United States of America, as *Gryllus* #45 [species identified in Weissman and Gray (2019: 54)], parasitoid as *O. ochracea*); Weissman and Gray (2019: 61, record from Matagorda County, Texas, United States of America, parasitoid as *O. ochracea*).

Gryllus (Gryllus) integer Scudder, 1901 (Gryllidae, Gryllinae, Gryllini)

Cade (1975: 1312, record from Austin, Travis County, Texas, United States of America, parasitoid as *Euphasiopteryx ochracea* [=Ormia ochracea (Bigot)]); Cade (1984: 226, record [artificial infestation] from San Antonio, Bexar County, Texas, United States of America, parasitoid as *E. ochracea* [=O. ochracea]); Adamo (1998: 530, record [artificial infestation] from Halifax, Nova Scotia, Canada, parasitoid as O. ochracea); O'Hara and Gray (2004: 171, record from Holbrook, Navajo County, Arizona, United States of America [host species; however, may actually be *Gryllus* (*Gryllus*) armatus Scudder, see Weissman and Gray (2019: 110)], parasitoid as *Exoristoides johnsoni* Coquillett); Hedrick and Kortet (2006: 1113, records from Aguila (Maricopa County, Arizona), and Davis (Yolo County, California), United States of America, parasitoid as O. ochracea); Weissman and Gray (2019: 110, record from Fallon, Churchill County, Nevada, United States of America, parasitoid as *E. johnsoni*).

Gryllus (Gryllus) lightfooti Weissman & Gray, 2019 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 213, records from Alamo Lake (La Paz County), Brown Canyon (Pima County), Mount Graham (Graham County), Painted Rock Petroglyph Site (Maricopa County), and Willcox Playa (Cochise County), Arizona, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) lineaticeps Stål, 1861 (Gryllidae, Gryllinae, Gryllini)

Wagner (1996: 280, record from Tucker's Grove County Park, Santa Barbara, Santa Barbara County, California, United States of America, parasitoid as *Ormia ochracea* (Bigot)); Paur and Gray (2011: 147, record

from King Gillette Ranch near Malibu Creek State Park, Santa Monica Mountains, Los Angeles County, California, United States of America, parasitoid as *O. ochracea*); Beckers and Wagner (2012: 470, record from Rancho Sierra Vista, Santa Monica Mountais, Ventura County, California, United States of America, parasitoid as *O. ochracea*).

Gryllus (Gryllus) longicercus Weissman & Gray, 2019 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 226 and 229, records from Kitt Peak (Pima County), and Palm Canyon, Kofa National Wildlife Refuge (Yuma and La Paz Counties), Arizona, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) montis Weissman & Gray, 2019 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 204, records from Prescott National Forest (Yavapai County, Arizona) and Reserve (Catron County, New Mexico), United States of America, parasitoid as *Exoristoides johnsoni* Coquillett, and from Miller Canyon (Huachuca Mountains, Cochise County, Arizona), United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) multipulsator Weissman, 2009 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 83, record from Yuma, Yuma County, Arizona, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) ovisopis Walker, 1974 (Gryllidae, Gryllinae, Gryllini)

Wineriter and Walker (1990: 625, record [artificial infestation] from Gainesville, Alachua County, Florida, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) pennsylvanicus Burmeister, 1838 (Gryllidae, Gryllinae, Gryllini)

Aldrich (1932: 24, record from Capa, Jones County, South Dakota, United States of America, as *G. abbreviatus* Serville, parasitoid as *Exoristoides johnsoni* Coquillett).

Gryllus (Gryllus) rubens Scudder, 1902 (Gryllidae, Gryllinae, Gryllini)

Wineriter and Walker (1990: 625, record from Gainesville, Alachua County, Florida, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) saxatilis Weissman & Gray, 2019 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 244, records from Fallon (Churchill County) and Winnemucca (Humboldt County), Nevada, United States of America, parasitoid as *Exoristoides johnsoni* Coquillett, and from Corn Springs and Palm Desert, Riverside County, California, United States of America, parasitoid as *Ormia ochracea* (Bigot).

Gryllus (Gryllus) staccato Weissman & Gray, 2019 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 186, records from Agua Fria and Cordes Junction (Yavapai County), Catalina and Robles Junction (Pima County), and Wenden (La Paz County), Arizona, United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) texensis Cade & Otte, 2000 (Gryllidae, Gryllinae, Gryllini)

Vincent and Bertram (2009: 599, records from Austin and Smithville, Bastrop County, Texas, United States of America, parasitoid as *Ormia ochracea* (Bigot)); Weissman and Gray (2019: 96, records from Bentsen-Rio Grande Valley State Park (Hidalgo County), Brownsville (Cameron County), Del Rio (Val Verde County), and Schulenburg (Fayette County), Texas, United States of America, parasitoid as *O. ochracea*).

Gryllus (Gryllus) veletis (Alexander & Bigelow, 1960) (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 145, records from Chadron (Dawes County, Nebraska), Road to Zion Narrows (Kane County, Utah), and Sioux Falls (Minnehaha County, South Dakota), United States of America, parasitoid as *Exoristoides johnsoni* Coquillett).

Gryllus (Gryllus) vocalis Scudder, 1901 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 161, records from Fallon, Churchill County, Nevada, United States of America, parasitoid as *Exoristoides johnsoni* Coquillett, and from Agua Fria (Yavapai County, Arizona), Ballona Wetlands (Los Angeles County, California), Fallon (Churchill County, Nevada), and Sedona (Yavapai and Coconino Counties, Arizona), United States of America, parasitoid as *Ormia ochracea* (Bigot)).

Unidentified *Gryllus* Linnaeus, 1758 (Gryllidae, Gryllinae, Gryllini)

Woodley and Judd (1998: 659, record from Gainesville, Alachua County, Florida, United States of America, parasitoid as unidentified *Anisia* Wulp).

Hapithus (Orocharis) luteolira (Walker, 1969) (Oecanthidae, Podoscirtinae, Hapithidi, Hapithini)

Walker et al. (1996: 381, record from Florida, United States of America, as *Orocharis luteolira*, parasitoid as *Ormia dominicana* Townsend, 1919).

Unidentified Grylloidea

Aldrich (1928: 301, record from Kansas, United States of America, as cricket, parasitoid as *Oedomatocera gilvipes* [=*Anisia gilvipes* (Coquillett)]).

Neotropical Region

Anurogryllus (Urogryllus) toledopizai (de Mello, 1988) (Gryllidae, Gryllinae, Gryllini)

Gudin et al., present records from Canguçu, Rio Grande do Sul, Brazil, parasitoid as unidentified *Calodexia* Wulp, and São João da Reserva, São Lourenço do Sul, Rio Grande do Sul, Brazil, parasitoid as *Ormia ochracea* (Bigot).

Unidentified *Anurogryllus* Saussure, 1877 (Gryllidae, Gryllinae, Gryllini)

Fowler and Mesa (1987: 408, record from Ipeúna, São Paulo, Brazil, parasitoid as *Euphasiopteryx depleta* [=Ormia depleta (Wiedemann, 1830)]); Fowler (1988: 398, record [artificial infestation] from Rio Claro, São Paulo, Brazil, parasitoid as *E. depleta* [=O. depleta]).

Unidentified *Aracamby* de Mello, 1992 (Phalangopsidae, Luzarinae, Aracambiae)

Gudin et al., present records from Caraguatatuba, São Paulo, Brazil, parasitoid as unidentified *Anisia* Wulp, and from Matinhos, Paraná, Brazil, parasitoid as *Calodexia* cf. *flavipes* (Schiner).

Gryllus (Gryllus) assimilis (Fabricius, 1775) (Gryllidae, Gryllinae, Gryllini)

Tavares (1965: 21, record from Ribeirão Preto, São Paulo, Brazil, parasitoid as *Euphasiopteryx ochracea* [=*Ormia ochracea* (Bigot)]).

Gryllus (Gryllus) cohni Weissman, Rentz & Alexander, 1980 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 168, record from San Carlos Bay, Baja California Sur, Mexico, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) multipulsator Weissman, 2009 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 168, record from San Carlos Bay, Baja California Sur, Mexico, parasitoid as *Ormia ochracea* (Bigot)).

Gryllus (Gryllus) staccato Weissman & Gray, 2019 (Gryllidae, Gryllinae, Gryllini)

Weissman and Gray (2019: 168, record from San Carlos Bay, Baja California Sur, Mexico, parasitoid as *Ormia ochracea* (Bigot)).

Unidentified *Gryllus* Linnaeus, 1758 (Gryllidae, Gryllinae, Gryllini)

Fowler and Mesa (1987: 408, record [artificial infestation] from Rio Claro, São Paulo, Brazil, parasitoid as *Euphasiopteryx* ochracea [=Ormia ochracea (Bigot)]).

Unidentified *Eidmanacris* Chopard, 1956 (Phalangopsidae, Luzarinae)

Gudin et al., present record from Apiaí, São Paulo, Brazil, parasitoid as *Calodexia* cf. *fasciata* Curran.

Unidentified *Eneoptera* Burmeister, 1838 (Gryllidae, Eneopterinae, Eneopterini)

Rettenmeyer (1961b: 1027, record from Canal Zone Biological Area, Barro Colorado Island, Panama, parasitoid as unidentified *Calodexia* Wulp, near *C. agilis* Curran, 1934a, or *C. interrupta* Curran, 1934a).

Guabamima lordelloi de Mello, 1993 (Phalangopsidae, Luzarinae)

Gudin et al., present record from Mucuri, Bahia, Brazil, parasitoid as *Calodexia* cf. *venteris* Curran.

Unidentified *Pizacris* Souza-Dias & Desutter-Grandcolas, 2015 (Phalangopsidae, Luzarinae)

Gudin et al., present record from São Fidélis, Rio de Janeiro, Brazil, parasitoid as *Calodexia* cf. *insolita* Curran.

Ponca venosa Hebard, 1928 (Gryllidae, Eneopterinae, Lebinthini)

Rettenmeyer (1961b: 1026, record from Canal Zone Biological Area, Barro Colorado Island, Panama, parasitoid as *Calodexia interrupta* Curran).

Unidentified Grylloidea

Rettenmeyer (1961a: 15, record from Canal Zone Biological Area, Barro Colorado Island, Panama, parasitoid as unidentified *Calodexia* Wulp).

Unidentified Phalangopsidae

Rettenmeyer et al. (2011: 286, record from Trinidad, Trinidad and Tobago, host as cricket [probably *Luzara* Walker, 1869], parasitoid as unidentified *Calodexia* Wulp); Gudin et al., present record from Salesópolis, São Paulo, Brazil, parasitoid as *C.* cf. *flavipes* Curran.

Discussion

Based on the host catalog, there are at least three types of oviposition strategies used by tachinids that are parasitoids of true crickets: indirect oviposition with ovoviviparous species that lay incubated membranous eggs with well-developed first-instar larvae on the host's path (e.g., *Exoristoides* and *Ormia*) (Lehmann 2003, O'Hara and Gray 2004), oviparous species that deposit incubated microtype eggs on the host's food that are subsequently ingested by the host (e.g., *Anisia*) (Wood and Zumbado 2010), and direct oviposition with oviparous species that lay incubated membranous eggs with well-developed first-instar larvae directly on the cuticle of the host (e.g., *Calodexia*) (Rettenmeyer et al. 2011). Each oviposition strategy enables exploitation of different groups of true crickets.

Ormiini flies, including *Ormia* species, are frequently reared from mole crickets (Gryllotalpidae) and katydids (Tettigoniidae), which sing at high frequencies (Lehmann 2003). Only three species of *Ormia* seem to have adapted to detect lower frequency calls of true crickets: *O. depleta*, *O. dominicana*, and *O. ochracea* (Table 1). Four cricket genera from Gryllidae and Oecanthidae are

parasitized by Ormia species: Hapithus Uhler, 1864, Anurogryllus Saussure, Gryllus Linnaeus, and Teleogryllus Chopard, 1961. All of them are recognized as good singers with sound records used for species descriptions and bioacoustic studies (e.g., Walker 1977, Riede 1998, Gwynne 2001, Otte and Pérez-Gelabert 2009, Redü and Zefa 2017). Anurogryllus species are known for their long and loud trills, whereas the other three genera usually have species with calls characterized by chirps. Regarding the distribution of the three *Ormia* species recorded above, Gray et al. (2019) estimated the origin of O. ochracea in southern Mexico and/or the Gulf region of the United States of America (USA), with widespread distribution to the western USA and posterior introduction to Hawaii. Tavares (1965) extended its distribution southward, providing the first record of its occurrence in Brazil. Ormia depleta is a Neotropical species distributed in Brazil and Peru, with one record in Honduras in Central America (Sabrosky 1953, Tavares 1953), and O. dominicana is widely distributed in Central America and the southern United States (Sabrosky 1953).

In the genus *Exoristoides*, only *E. johnsoni* (Fig. 8A–D) has been reared from true crickets, but other species parasitize cockroaches (O'Hara 2002). Exoristoides johnsoni is widely distributed in the United States and southern Canada, with some records in Mexico (O'Hara 2002). Although E. johnsoni has a host range similar to that of O. ochracea (Table 1), these flies do not have morphological modifications to locate their hosts by sound. *Exoristoides* species have the same type of eggs and first-instar larvae as Ormiini and other tribes of the subfamily Tachininae (O'Hara and Gray 2004, Stireman et al. 2019), but their behavior is still unknown. Despite this, the behavior of species with similar oviposition strategies that parasitize orthopteroids has already been verified, such as *Tri*arthria setipennis (Fallén, 1810), which is a parasitoid of earwigs (Dermaptera: Forficulidae) (Kuhlmann 1995, Tschorsnig 2017). Kuhlmann (1995) demonstrated that cardboard disks filled with earwig's scent and feces induce the oviposition of gravid females of *T. setipennis*, which suggests the existence of chemical substances involved in the search for the host. It is possible that a similar process may be observed in *Exoristoides* females, but further studies are necessary to clarify this.

Among these four genera, *Anisia* is the most difficult group to investigate because its taxonomy remains obscure and requires revision (Wood 1985). From the Nearctic region, only A. gilvipes (Fig. 8E-H) was reared from a true cricket and identified to species level (Aldrich 1928). Anisia species have also been reared from cockroaches, earwigs, grasshoppers (Acrididae), and camel crickets (Rhaphidophoridae) (Gemeno et al. 2002). Wood and Zumbado (2010) recorded the behavior of the Nearctic species A. flaveola (Coquillett, 1897), which deposits minute, unpigmented, and incubated eggs on the host's food. Similar eggs were also recorded in A. facialis (Townsend) by Parker (1953) and in A. aberrans (Townsend, 1935) and A. fumipennis (Thompson, 1968) by Thompson (1968). Anisia species have been recorded in Gryllus and Aracamby (Table 1), suggesting that singing is not necessarily the main cue used by gravid females to find their hosts. However, even though Aracamby males cannot produce calling songs as they lack important traits of the stridulatory apparatus on the forewings, such as the mirror and harp (de Mello 1992), they are capable of performing low-frequency courtship songs (de Mello 2007). This raises the question of whether *Anisia* females are able to detect low-frequency sounds produced by their orthopteroid hosts. On the other hand, the use of chemical cues by Anisia females is also possible. As orthopteroids are normally generalists, the main cues used by *Anisia* females probably do not derive from

the host's diet but from the host itself. Similar to what was hypothesized for *Exoristoides*, it is possible that *Anisia* females use chemical cues derived from their hosts, as the presence of chemical communication between crickets is known (e.g., Bell 1980, Thomas and Simmons 2008, Stamps and Shaw 2019). *Anisia* is the only blondeliine genus known to date that has this oviposition strategy. Microtype eggs also occur in the dufouriine genus *Oestrophasia* Brauer & Bergenstamm, 1889, and most notably in the tribe Goniini (Marini and Campadelli 1994, de Santis and Nihei 2022), but the morphology of their eggs is completely different.

Calodexia is a diverse Neotropical genus associated with army ants whose females are frequently found perched on the foliage ahead of advancing ants, waiting for fleeing orthopteroids (Rettenmeyer et al. 2011). Due to the extreme sexual dimorphism found in the genus, the association of males and females is a difficult task. Calodexia species have been reared only from cockroaches and crickets (Rettenmeyer 1961b). Gravid females quickly dart toward the fleeing host, laying incubated membranous eggs with well-developed first-instar larvae directly on the cuticle of the host (Rettenmeyer et al. 2011). As Calodexia species are closely associated with army ants, females rely mainly on visual cues to search for hosts. This kind of search enables them to exploit several groups of true crickets, either chirping or silent species. For instance, males of Aracamby, Eidmanacris, and Pizacris have no forewings modified for stridulation (de Mello 1992, Campos et al. 2017, Souza-Dias et al. 2015); on the other hand, males of Anurogryllus, Eneoptera Burmeister, Ponca Hebard, 1928, and Guabamima de Mello, 1993, have forewings modified for sound production and propagation. These groups are usually found in litter, which exposes them to army ants and, consequently, to Calodexia females.

Conclusions

In this study, seven new host records in Gryllidae and Phalangopsidae species were recorded from Brazil for the first time. At least ten species of Tachinidae in the New World genera *Anisia*, *Calodexia*, *Exoristoides*, and *Ormia* are parasitoids of Gryllidae, Oecanthidae, and Phalangopsidae species. Only *Ormia* species use phonotactic cues to locate their singing hosts. *Anisia* and *Exoristoides* species may rely on chemical cues derived from the host, whereas *Calodexia* species locate their hosts visually. The host range of *Calodexia* species seems to be wider than that of species in the three other genera, as the association with army ants allows them to exploit the diversity of cricket species that live in litter. Further studies on the biology of *Anisia* and *Exoristoides* species are necessary to improve our knowledge of Tachinidae–Orthoptera interactions.

Acknowledgments

We thank the Instituto de Biociências da Universidade de São Paulo (IBUSP) and Silvio Nihei (IBUSP) for research support; James O'Hara and Shannon Henderson (CNC) for kindly providing pictures of *Anisia gilvipes* and *Exoristoides johnsoni* specimens deposited in CNC; and Pedro Souza-Dias for kindly providing pictures of *Pizacris carioca* to illustrate the genus. We also thank Pedro Souza-Dias and Deivys Moises Alvarez-Garcia for their valuable comments and suggestions on an earlier version of the manuscript. FMG thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, proc. 152937/2022-6) for research support. LDC and DRR thank the Orthopterists Society and the Orthoptera Species File for their support.

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